Chromosomal banding patterns of the Holarctic rodents, *Clethrionomys rutilus* and *Microtus oeconomus*

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Biologists have long been aware of close similarities between the mammalian faunas of northern Eurasia and northern North America (Flerov 1967; Rausch 1953, 1963; Sushkin 1925; Tugarinov 1934). This similarity is particularly strong between species of tundra and taiga ecosystems (Hoffmann and Taber 1967; Hoffmann 1974). Among the species having Holarctic distributions, the boreal red-backed vole, *Clethrionomys rutilus* (Pallas), and the tundra vole, *Microtus oeconomus* (Pallas) (Rausch, op. cit.), of the subfamily Arvicolinae (= Microtinae) (Kretzoi 1962; Repenning 1968), have wide distributions in Eurasia where they inhabit, but are not restricted to, tundra (Ognev 1950; Corbet 1966). East of the Bering Strait, however, the two voles occur only in northwestern North America, and appear in some areas to have narrower habitat niches than Eurasian populations (Bee and Hall 1956; Cowan and Guiget 1956). This pattern of distribution suggests that both species are relatively recent trans-Beringian immigrants into North America from Siberia (MacPherson 1965; Rausch 1963). North American populations are now isolated from conspecifics in eastern Siberia by the flooding of the Bering land bridge about 12,800 years ago as sea level rose (Hopkins 1967). Some of the differences between Alaskan and eastern Siberian populations may have arisen in this period of separation.

Published descriptions of the karyotypes of these voles permitted comparisons of gross morphology of their chromosomes. The diploid number of *Microtus oeconomus* (2n = 30) in Eurasia (Makino 1950; Matthey 1952) is the same as in Alaskan voles (Rausch and Rausch 1968) and the karyotypes are grossly indistinguishable. The same is true of *Clethrionomys rutilus* (2n = 56) in Eurasia (Makino 1952; Shimba et al. 1969) and Alaska (Rausch and Rausch 1975).

Recently it has become possible to make more detailed comparisons of chromosomal homologies, by comparing patterns of banding elicited in chromosomes by certain treatments (Caspersson et al. 1970; Arrighi and Hsu 1971). Among these, the technique of staining chromosomes with Giemsa, after treatment with trypsin (Seabright 1972) produces well-defined bands, and has been increasingly employed in stdies of chromosomal homologies. Giemsa banding studies have already been made of certain Holarctic taxa; karyotypes of the Siberian long-tailed ground squirrel, *Spermophilus undulatus* (Pallas), and the North American *S. columbianus* (Ord) have been compared (Nadler et al. 1975), as have Old and New World *Ovis* (Nadler et al. 1973, 1974). Chromosomal patterns appeared quite conservative, and no major differences in patterns could be found between homologous arm segments in these taxa.

This paper describes the Giemsa band patterns of *Clethrionomys rutilus* from Alaska and Asia and *Microtus oeconomus* from several Alaskan localities. We also make comparisons with North American *C. gapperi* (Vigors), Eurasian *C. glareolus* (Schreber), and preliminary comparisons with Eurasian *C. rufocanus* (Sundevall).

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Materials and Methods

The following specimens were examined: *Clethrionomys gapperi gapperi* (Vigors), Wisconsin. Vilas Co., 5 mi. northeast of Lac du Flambeau, 1 male; *Clethrionomys gapperi galei* (Merriam), Wyoming, Fremont Co., 11 miles south and 8½ miles west of Lander, 1 male; *Clethrionomys rutilus dawsoni* (Merriam), Alaska, Tikchick Lake, 60 miles north of Dillingham, 1 male; Alaska Peninsula, 15 miles north of Egegik, 1 male; vicinity of Anchorage, 2 females and 2 males; Healy, 1 female and 1 male; *Clethrionomys rutilus jacutensis* (Vinogradov), U.S.S.R., Yakutskaya ASSR, Yakutsk, 1 female and 1 male; *Clethrionomys rutilus amurensis* (Schrenk), U.S.S.R., Primorskii Krai, Ussuriisk, 1 female; *Clethrionomys glareolus glareolus* (Schreber), U.S.S.R., Tulskaya Oblast, 12 miles north of Tula, 1 female and 1 male; *Microtus oeconomus macfarlani* Merriam, Alaska, Fairbanks, mile 2, Goldstream Road, 1 male; *Microtus oeconomus kadiacensis* Merriam, Alaska, Izembek Lagoon, 10 miles north of Cold Bay, 1 female; *Microtus oeconomus operarius* (Nelson), Alaska, Bettles, 3 females and 3 males; *Microtus oeconomus yakutatensis* Merriam, Alaska, Homer, 2 females and 2 males. Nomenclature and distribution of subspecies of *M. oeconomus* are based on Rausch (1953).

Most chromosomal preparations were made from bone marrow after colcemide or Velban induced mitotic inhibition. Hypotonic treatment with 0.075M KCl, fixation in 3:1 absolute ethyl alcohol: acetic acid, and flame drying were followed by the Seabright (1972) procedure for developing Giemsa-bands induced by the action of trypsin. Skin biopsies grown in tissue culture through the courtesy of Dr. T. C. Hsu and Ms. Linda Shirley, M. D. Anderson Hospital and Tumor Institute, Houston, Texas, provided the source of other chromosome preparations that were treated by the Seabright (1972) method for G-banding.

Idiograms were constructed only after comparing many G-band karyotypes, and represent a composite view of each taxon; frequently a single karyotype does not display all bands depicted in the idiogram.

Results

All North American populations of *Clethrionomys rutilus* had 2n = 56. All karyotypes were identical, containing 26 pairs of telocentric and one pair of small metacentric autosomes, an X chromosome that was the largest acrocentric of the entire complement, and a small nearly metacentric Y chromosome (Fig. 1). Comparison of Giemsa-band patterns from these North American population yielded similar banding patterns that together were utilized for preparation of the idiogram depicted in Figure 2. The X chromosome was readily identified by its large size and unique

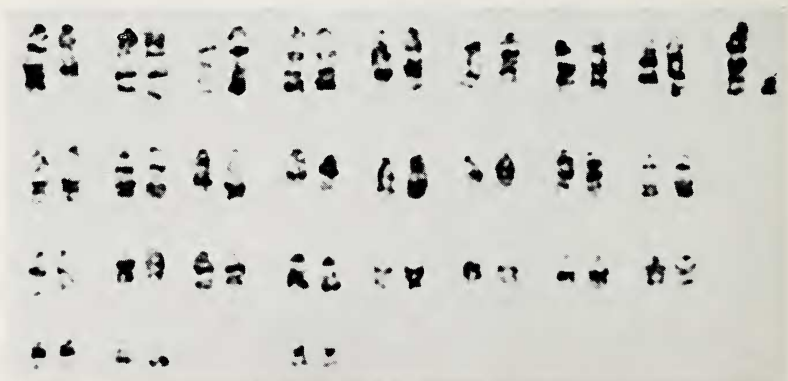

Fig. 1. Karyotype of a male *Clethrionomys rutilus dawsoni* from the Alaska Peninsula illustrating typical Giemsa-banding. The large acrocentric X and small nearly metacentric Y are placed at the right of the top row, and the single pair of small metacentric biarmed autosomes in placed at the right of the bottom row

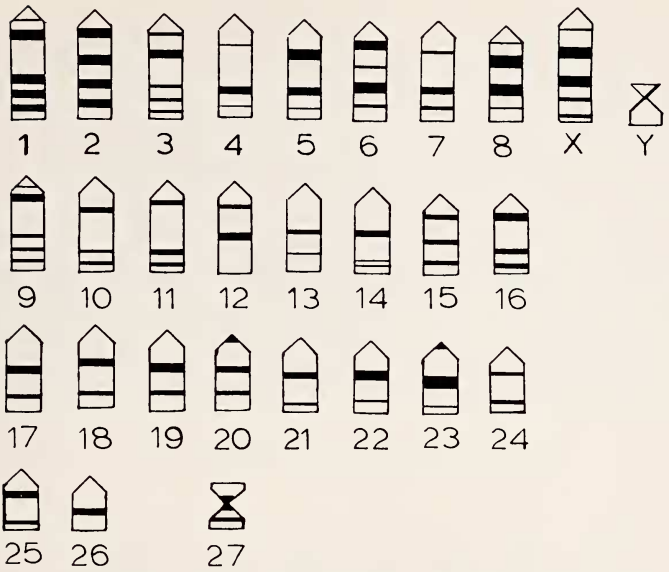

Fig. 2. Idiogrammatic representation of the Giemsa-band pattern of North American *C. rutilus* (chromosomal arrangements as in Fig. 1)

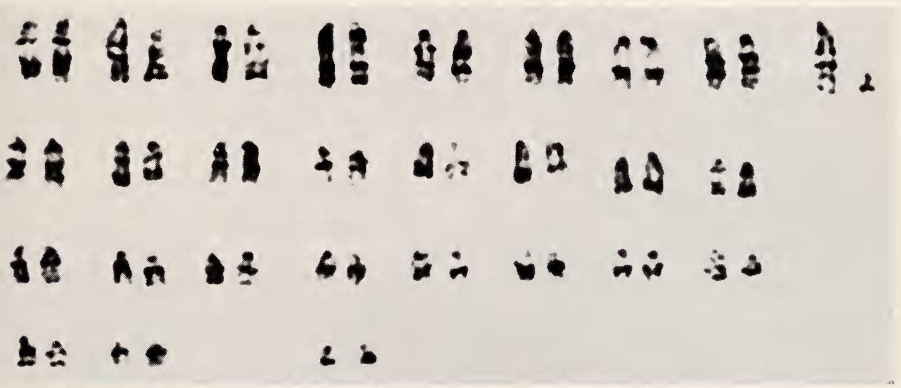

Fig. 3. Karyotype of a male *C. gapperi gapperi* from Wisconsin illustrating typical Giemsa-band pattern (chromosomal arrangements as in Fig. 1)

band pattern and the Y chromosome was distinguishable from the small pair of biarmed autosomes by its lack of bands.

Both subspecies of *Clethrionomys gapperi* (Fig. 3) also displayed 2n = 56 and karyotypes and G-band patterns indistinguishable from those of Alaskan *C. rutilus*, except that the Y chromosome was subtelocentric to telocentric.

Clethrionomys rutilus (Fig. 4) and *Clethrionomys glareolus* from Eurasia were both characterized by 2n = 56 and possessed autosomes morphologically similar to North American *C. rutilus* and *C. gapperi*. G-bands were similar in Eurasian *C. rutilus* and *C. glareolus*, although both inter- and intraspecific comparison of pairs 7 and 8; 9 and 10; 18, 19 and 20; 21 and 22; and 24 and 25 were difficult to assess because patterns within these groups were quite similar. Staining of the biarmed

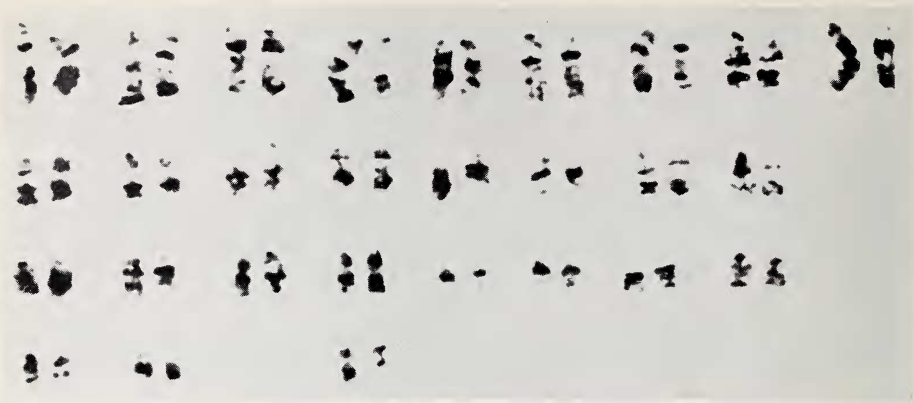

Fig. 4. Giemsa-banded karyotype of a female *C. rutilus jakutensis* from Yakutskaya ASSR, USSR (chromosomal arrangements as in Fig. 1)

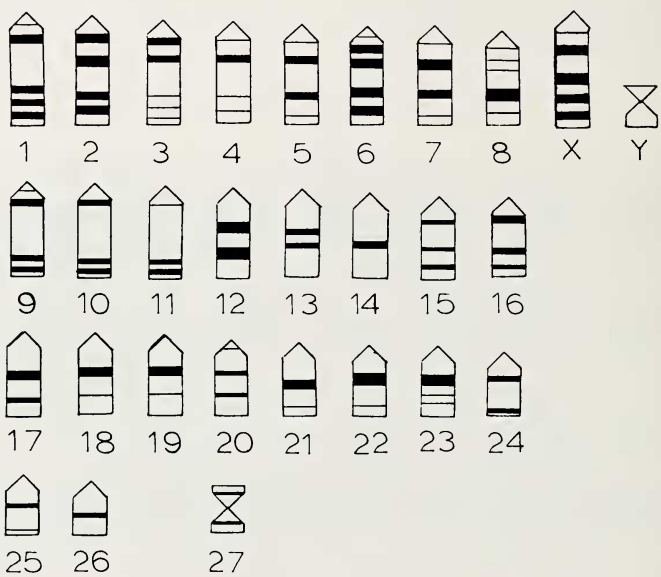

Fig. 5. Provisional idiogram of Giemsa-banding in Eurasian *C. rutilus* and *C. glareolus*, based on specimens from Yakutskaya and Tulskaya oblasts respectively, USSR (Chromosomes arranged as in Fig. 1)

pair of autosomes was faint and the idiogrammatic representation of that pair is tentative. A provisional idiogram reflecting the G-banding of Eurasian *Clethrionomys* is presented in Fig. 5.

Comparison of idiograms from North American and Eurasian *Clethrionomys* demonstrates basically similar patterns and therefore presumed chromosomal homology involving pairs 1–3, 5, 8, 10–13, 15–26, and the X and Y chromosomes. Slight differences observed were the presence of an additional faintly staining band (Eurasian pairs 4–7), the absence of one or two faintly staining bands (Eurasian pairs, 9 and 14) and the possible presence of a second band in Eurasian pair 27, although

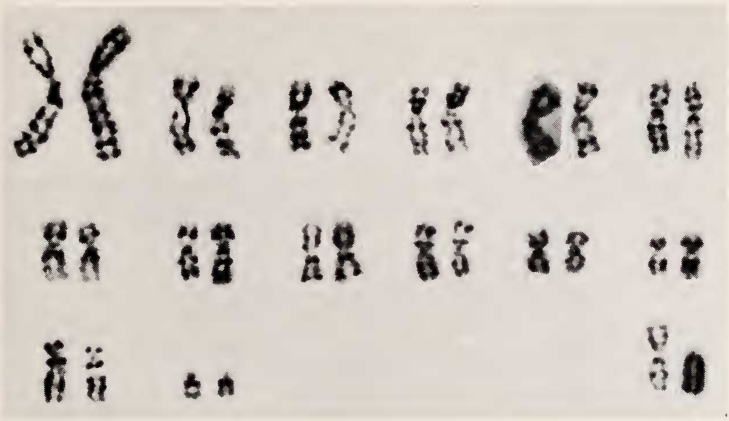

Fig. 6. Karyotype of a male *Microtus oeconomus macfarlani* from Fairbanks, Alaska, illustrating a typical Giemsa-band pattern. Sex chromosomes are placed at the lower right.

Lyapunova regarded these differences as probably artifacts resulting from differences in chromosome contraction, trypsin effect, and staining.

A published G-band karyotype of *Clethrionomys rufocanus* from Japan (Mascarello et al. 1974) also shares many similarities with North American *Clethrionomys;* 15 of 27 autosomal pairs and the X chromosome appear homologous whereas 12 are either indeterminate or differ due to the lack of minor bands in *C. rufocanus.* The Y chromosome of *C. rufocanus* is subtelocentric to telocentric (Hsu and Benirschke 1967–71, 119), thus resembling that of *C. gapperi.*

All populations and subspecies of *Microtus oeconomus* uniformly had 2n=30 and karyotypes comprised of 12 pairs of metacentric or submetacentric autosomes, one pair of distinctive subtelocentric autosomes, one small pair of telocentric autosomes, a submetacentric X and an acrocentric Y chromosome (Figs. 6 and 7). *M. oeconomus* G-band patterns possessed no close resemblances to the patterns of *Clethrionomys.*

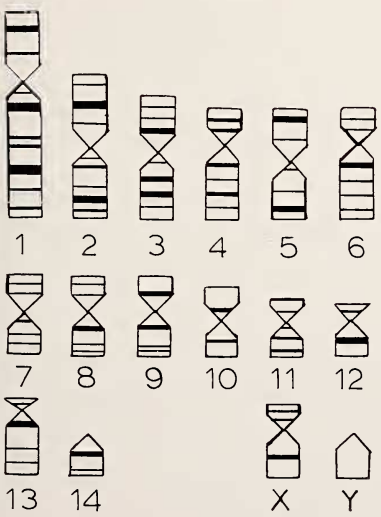

Fig. 7. Idiogram of Giemsa-banding in populations of Alaskan *M. oeconomus* ssp. (chromosomal arrangement as in Fig. 6)

Discussion

All species of *Clethrionomys* inhabiting the Holarctic have similar karyotypes (2n=56); North American *C. rutilus, C. gapperi,* and *C. occidentalis* (Hsu and Benirschke 1967–1971, 171; Rausch and Rausch 1975), and Eurasian *C. rutilus, C. glareolus, C. rufocanus* (Hsu and Benirschke 1967–1971, 119, 172; Makino 1952) and *C. frater* (Orlov 1974). The only reported variations are 1. in the morphology of the smallest pair of autosomes which ranges from metacentric to submetacentric; 2. differences in Y chromosome structure ranging from metacentric to telocentric; and 3. chromosome polymorphism due to centric fusion

in Alaskan *C. rutilus albiventer* Rausch and Rausch 1975). Comparison of G-band patterns now generally confirms the chromosomal uniformity originally suggested by conventional methods of chromosome analysis. The absence of differences in banding patterns of Alaskan *C. rutilus* derived from four widely separated populations and the lack of differentiation between these populations and the two specimens of *C. gapperi,* each representing a different subspecis, argue strongly that chromosomal structure has remained intact since divergence of these several populations from a common ancestral stock. Indistinguishable banding patterns also link *C. glareolus* and *C. rutilus* from Eurasia.

Only minor differences, perhaps entirely due to variations in individual interpretation or technical artifacts, distinguish Siberian and North American *C. rutilus,* suggesting that karyotypic stability has been maintained since the time of their geographic separation by inundation of the Bering Strait 12,800 years ago. Eurasian *C. glareolus* and North American *C. gapperi* also display patterns which indicate a high degree of autosomal homology, although differences in Y chromosome structure exist.

The grouping of species of *Clethrionomys* into two groups based on the presence of telocentric or metacentric Y chromosomes was discussed by Rausch and Rausch (1975). Our studies confirm the presence of nearly metacentric Y chromosomes in *C. glareolus* and Holarctic *C. rutilus* and a nearly telocentric Y in *C. gapperi.* However the similarities in banding patterns between North American *C. rutilus* and *C. gapperi,* together with the unknown meiotic significance of the morphological differences in the Y chromosomes do not provide very solid ground for taxonomic speculation at this time.

Given this chromosomal similarity, it is not surprising that certain taxa of red-backed voles can interbreed. Grant (1974) paired English *C. glareolus* and *C. gapperi* from Quebec, Canada, and they produced hybrid offspring that were fertile when backcrossed. These interspecific pairs interbred as frequently as intraspecific pairs of both species, and produced litters of similar size. However, F_1 hybrid offspring had higher mortality rates, especially prior to weaning, and "two short attempts to produce an F_2 generation from them were unsuccessful." Grant (op. cit.) concluded that reproductive isolation between *C. glareolus* and *C. gapperi* was only partial, but that "if they ever made contact in nature, the most likely outcome appears to be selection against hybrids leading to full speciation", and recommended that they be considered semispecies (sensu Mayr 1963) and retain their separate names.

In contrast, *C. glareolus* and Eurasian *C. rutilus* produce sterile male offspring when crossed (Spannhof 1960; Rauschert 1963), even though they exhibit the same degree of chromosomal homology as revealed by G-band patterns. Apparently the level of resolution provided by G-banding is not sufficiently fine to allow predictions concerning degree of genetic compatibility.

As in the case of *C. rutilus* (Rausch 1963), a trans-Beringian distribution of forest-dwelling *C. gapperi/glareolus* may have existed. This probably was at a much earlier time than in the case of *C. rutilus,* perhaps during the mid-Pleistocene (Mindel-Kansan), about 600,000 years ago when a forest climate may have existed on some part of the land bridge (Hoffmann, ms). Likewise, the date of evolutionary divergence of the more specialized boreal *C. rutilus* was probably later than that time when the population ancestral to the two forest species, *C. gapperi* and *C. glareolus,* had a Holarctic distribution, unless one postulates that *C. rutilus* is instead ancestral to the forest species. This seems to us less likely, for it would postulate that the ancestral *Clethrionomys* was a more specialized *rutilus*-like form that gave rise to a less-specialized *glareolus-gapperi*-like form.

If one accepts this reasoning, then the taxa that have been separated for a longer time (*C. gapperi, C. glareolus)* have less-developed isolating mechanisms than the taxa that have been separated for a shorter time (*C. glareolus, C. rutilus*). In geographic isolation, *C. glareolus* and *C. gapperi* would have been under similar selective pressures to adapt to their similar forest habitats in Eurasia and North America respectively, and behavioral or genetic mechanisms of reproductive isolation between them would have developed only by chance. On the other hand, the divergence of *C. rutilus,* probably from *C. glareolus,* led to the former becoming adapted to more boreal habitats, including tundra, and, since geographic isolation was not maintained, to selection favoring the development of reproductive isolation. In other words, geographic allopatry and similar ecological niches have resulted in a low rate of evolutionary divergence, whereas geographic sympatry combined with adaptation to different niches produced a more rapid evolutionary divergence. Grant (op. cit) has adduced a similar argument to account for different rates of evolution between *C. glareolus* and *C. gapperi* on the one hand, and British "mainland" and Skomer island populations of *C. glareolus* on the other.

Fewer homologies were noted between the G-banded chromosomes of Eurasian *C. rufocanus* (Mascarello et al. 1974) and Eurasian *C. glareolus* and *C. rutilus* or the North American taxa. These differences are difficult to resolve without access to more *C. rufocanus* material but they may reflect chromosomal divergence that plays a role in the maintenance of reproductive isolation between *C. rufocanus* and *C. rutilus,* well-differentiated taxa that are sympatric throughout most of their vast distribution (Ognev 1950), in contrast to the small degree of sympatry between *C. glareolus* and *C. rutilus,* and virtual parapatry between *C. rutilus* and *C. gapperi.* In fact, James Bee suggested that the latter two taxa may be conspecific (Bee and Hall 1956), although work in progress has now caused him to consider this less likely (Bee pers. comm.). Laboratory studies of cross-breeding in *C. gapperi* and North American *C. rutilus,* as well as more detailed studies of the zone of potential contact between the two species, are obviously needed.

Intraspecific karyotypic homology, as judged by G-banding, was also demonstrated in Alaskan populations of *Microtus oeconomus,* representing four subspecies. However, comparison of G-banding patterns of *Clethrionomys* and *Microtus* revealed only a few chromosomal pairs suggestive of homology.

Our data from *Clethrionomys* and *Microtus* parallel the chromosomal homology observed in the North American ground squirrel *C. columbianus* and Asian long-tailed ground squirrel *C. undulatus.* In those species similar G-banding was maintained for an estimated 100,000 years or more (Nadler et al. 1975). G-banding homologies in Eurasian and North American *Clethrionomys* provide added evidence for the existence of a Holarctic "Beringian" biogeographic region connected intermittently during its history by a "Bering Land Bridge" that permitted intercontinental dispersal of mammals (Guthrie and Matthews 1971).

Mascarello et al. (1974) have claimed remarkable interspecific homologies between G-banding patterns of the rodent genus *Neotoma* and such divergent genera as *Peromyscus* and *Rattus.* Our results support their contention that the maintenance of the arrangement of genetic material on chromosomes tends to be long enduring. In *Clethrionomys* such conservative fixation of chromosome structure may offer a distinct selective advantage when compared to the wide range of chromosomal diversity, 2n 17 to 62, seen in various species of *Microtus.*

Our studies of comparative G-banding in related species posed a number of conceptual and practical difficulties. First, how many specimens must be examined in order to characterize a taxon cytogenetically? Mascarello et al. (1974) stated that "demonstrating that G-banding patterns are consistent for all cells from an

individual or for all individuals from a species is not considered to be within the scope of this study". They cited Caspersson and coworkers (1972) who found no banding variations in human and some plant cells in support of their own analysis of single specimens from each taxon for their intergeneric comparison. Our present studies of North American arvicolines and our prior work on ground squirrels (Nadler et al. 1975) support the view that intraspecific chromosomal homogeneity is to be expected. Nevertheless, we found that several specimens from each taxon, each providing a number of cells favorable for analysis, were necessary to arrive at an acceptable idiogram representative of a specific banding pattern. Only by these means could the medium to small sized chromosomes be characterized, a group that Mascarello et al. (1974) also found most difficult to analyze. The difficulty we experienced in comparing one published karyotype from a single specimen of *C. rufocanus* with our material exemplifies these problems and makes the important question of presence or absence of cytogenetic divergence within *Clethrionomys* more difficult to answer.

A second problem relates to the degree of objectivity attainable in making banding comparisons, especially when material is limited or when the same worker does not examine all materials compared. In our experience, differences in banding patterns may often merely reflect subjective views of individual observers; when karyotypes were examined jointly, resolution of such issues as the presence or absence of faint bands or band placement were resolvable. These factors probably account, on the one hand, for the complete homogeneity described for North American *Clethrionomys*, and on the other, for the few differences appearing in the idiograms presented herein for Eurasian and North American *Clethrionomys*. Joint comparison of data in future taxonomic work should be encouraged, to circumvent such technical problems. Despite these difficulties, studies of G-banding in mammals are of value in systematic studies of many taxa including rodents (Mascarello et al. 1974), sheep and goats (Nadler et al. 1973, 1974) and primates (Lucas and Wallace 1973).

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Summary

The Giemsa-band patterns of the chromosomes of *Clethrionomys rutilus, C. glareolus, C. gapperi*, and *Microtus oeconomus* are described. Comparisons of banding patterns between Siberian and Alaskan *C. rutilus*, and between these *C. rutilus* populations, *C. glareolus*, and *C. gapperi* reveal only minor autosomal differences that are probably artifacts of fixation and/or interpretational differences. Problems of G-band interpretation are discussed. *C. rutilus and C. glareolus* both possess a nearly metacentric Y chromosome, while *C. gapperi* and *C. rufocanus* have a subtelocentric to telocentric Y. These chromosomal similarities are associated with the demonstrated ability of certain taxa of *Clethrionomys* to hybridize. *C. glareolus* and *C. gapperi*, isolated for a long time period but adapted to similar environments, have less-developed isolating mechanisms than do *C. glareolus* and *C. rutilus*, probably isolated for a shorter time, but in geographic contact, and adapted to different ecological niches. Chromosomal homologies among the Holarctic species studied *(C. rutilus, M. oeconomus)* lend additional support to the concept of a Beringian biogeographic region.

Zusammenfassung

Giemsa-Bandmuster der holarktischen Nagetiere, Clethrionomys rutilus (Pallas) und Microtus oeconomus (Pallas)

Die G-Bandmuster deuten an, daß die Chromosomen von Rötelmäusen, *C. rutilus* (Pallas), aus Alaska und Sibirien sich voneinander und von denen der Arten *C. gapperi* (Vigors) und *C. glareolus* (Schreber) durch geringe autosomale Merkmale unterscheiden, die möglicherweise Fixierungsartefakte darstellen. In ihren Autosomen stimmen diese *Clethrionomys*-Arten offensichtlich völlig überein. Es wurde bestätigt, daß zwei Gruppen durch die Form der Y-Chromosomen zu unterscheiden sind: metacentrisch bei *C. rutilus* und *C. glareolus;* subtelocentrisch bis telocentrisch bei *C. gapperi* und *C. rufocanus* (Sundevall). Artkreuzungen bei *Clethrionomys* spp. sind erfolgreich, aber die Männchen der F_1-Generation scheinen immer steril zu sein. Nordische Wühlmäuse, *Microtus oeconomus* (Pallas), zeigen anscheinend keine chromosomalen Unterschiede zwischen Alaska und Sibirien. *C. glareolus* und *C. gapperi* sind wahrscheinlich seit der vorletzten Glazialphase in Eurasien beziehungsweise in Nordamerika isoliert worden. Bei diesen allopatrischen Arten, die ähnliche Biotopansprüche aufweisen, sind Isolationsmechanismen vielleicht verhältnismäßig schwächer, als bei *C. glareolus* und *C. rutilus*. Bei den letzteren, die sich in einer weit ausgedehnten Kontaktzone treffen und verschiedene ökologische Nischen bewohnen, scheinen Isolationsmechanismen stärker entwickelt zu sein. Die Homologie der Chromosomen der untersuchten holarktischen *C. rutilus* und *M. oeconomus* stimmt mit der Vorstellung überein, daß Beringia ein Zentrum der Anpassung an die arktischen Existenz-Bedingungen war.

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